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THE EFFECT OF BURROWING SPECIES OF *PROCELLARIIDAE* ON THE NUTRIENT STATUS OF INLAND TUSSOCK GRASSLANDS ON MARION ISLAND

V. R. Smith
(Institute for Environmental Sciences, University of the Orange Free State, Bloemfontein)

Abstract

On inland slopes of Marion Island the dominant *Blechnum penna-marina* fern carpet is replaced by luxuriant *Poa cookii*-dominated tussock grassland communities in areas where bird species of the *Procellariidae* establish burrows. Soils under these tussock grasslands have considerably higher contents of inorganic nitrogen and, in proportion to their organic carbon contents, of total phosphorus than do soils under other island plant communities. Plants growing in tussock grassland communities possess higher contents of nitrogen, phosphorus, potassium, iron and, to a lesser extent, sodium than do plants of the same species occurring in non-tussock grassland areas. These higher soil and plant nutrient contents are ascribed to manuring by the birds.

Uittreksel

DIE INVLOED VAN *PROCELLARIIDAE* SOORTE OP DIE MINERALE STATUS VAN BINNELANDSE POLGRASLANDE OP MARIONEILAND

Op Marioneiland word die dominante *Blechnum penna-marina* varingbedekking van die binnelandse hange deur 'n welige polgrasgemeenskap van *Poa cookii* verdring in gebiede waar voëls van die *Procellariidae* nesmaak. Grond van die polgrasgemeenskappe bevat 'n hoër anorganiese stikstofinhoud en, in verhouding met die organiese koolstofinhoud, 'n hoër fosforinhoud as grond wat onder ander plantgemeenskappe voorkom. Plante van die polgrasgemeenskappe is ryker aan stikstof, fosfor, kalium en yster, en in 'n mindere mate natrium, as plante van dieselfde spesies wat in nie-polgrasgemeenskappe groei. Die hoër mineraalkonsentrasie in die plante en grond van die polgrasgemeenskappe word aan bemesting deur voëls toegeskryf.

Introduction

Communities of large tussock-forming grasses of which *Poa* species are usually the most important dominants are characteristic features of the vegetation of southern ocean islands (Wace, 1960). Because these communities are most often best developed on sea-facing slopes close to the shore they have been considered by some workers to be halophytic and dependent upon exposure to salt-spray (Skottsberg, 1912, 1942; Cour, 1959). In most southern islands, however, tussock grassland communities are generally associated with penguin rookeries, seal

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wallowing-grounds, albatross nests and other biotic influences (Taylor, 1975; Wace, 1960, 1961; Greene, 1964; Smith and Walton, 1975).

In the Maritime Antarctic Smith (1972) notes that *Deschampsia antarctica* Desv. on Signy Island (60° 43′S., 45° 38′W.), although not forming tussocks proper, is particularly luxuriant immediately below nests of snow petrels (*Pagodroma nivea* Forster) and cape pigeons (*Fulmarus capensis* L.) and also at the margins of areas disturbed by elephant seals (*Mirounga leonina* L.). In the sub-Antarctic region Greene (1964) mentions that although pure stands of closed tussock grassland on South Georgia (54° 16′S., 36° 36′W.) are best developed on gently sloping ground away from penguin and elephant seal colonies, on the steep hillsides of Bird Island (54°S., 38° 3′W.), colonies of black-browed and grey-headed albatrosses (*Diomedea melanophrys* Temminck and *D. chrysostoma* Forster) lead to the local development of open tussock and the manuring influence of these birds results in an increased lushness of the tussock. In Macquarie Island (54° 30′S., 158° 57′E.) tussock grasslands *Poa foliosa* Hook.f. forms different associations with several other plant species and the association occurring at any given site depends upon exposure to sea-spray, maturity of the soil and trampling effects of animals (Taylor, 1955; Gillham, 1961). In his summary of the factors affecting the occurrence of the *P. foliosa* associations, however, Taylor does not include biotic influences.

As early as the end of the last century Moseley (1892) stated that on Marion Island (46° 54′S., 37° 45′E.) "The grass (*Poa cookii* Hook.f.) is abundant everywhere, mingled with *Acaena* (*A. magellanica* (Lam.) Vahl.) and *Azorella* (*A. selago* Hook.f.)", and that "The plants are, no doubt, rendered especially luxuriant by the dung of the numerous sea-birds." Moseley also added the erroneous observation that "The *Poa cookii* nowhere forms tussocks." Huntley (1971) considers that the manuring influence of birds and seals is of more importance than salt-spray in determining the distribution of *Poa cookii* tussock grassland on Marion Island as stands of this community are frequently found several km from the coast, where salt-spray deposition is slight but where numerous burrows of nesting colonies of small petrels and prions (family *Procellariidae*) occur.

During the period 1971–4 an intensive investigation into the nutrient relationships of the plants and soils of Marion Island was carried out. In the course of this investigation it became obvious that there are marked differences in the soil and plant nutrient status of the inland tussock grassland communities and that of the other island plant communities. These differences, which are ascribed to the manuring influences of the burrowing bird species inhabiting the tussock grassland communities, are presented in this paper. As far as can be ascertained no previous investigations into the chemical aspects of the relationship between tussock grassland and the manuring influences of animals have been undertaken on islands of the southern ocean.

SITE AND METHODS

Descriptions of the climate, geology, topography and vegetation of Marion Island are provided in Van Zinderen Bakker Sr., Winterbottom and Dyer (1971) and Smith (1976). The analytical methods used in the determination of the mineral contents of the plants and the soils are outlined in detail in Smith (*l.c.*).

DISCUSSION AND RESULTS

Similar to those of many polar and circumpolar regions, the soils of Marion Island are deficient in nitrogen and phosphorus (Smith, 1976 and Table 1) and any mechanisms whereby these two elements are added to the soil system are manifested by marked increases in plant vitality and standing crop of the vegetation (Van Zinderen Bakker Jr., 1971). Areas surrounding elephant seal wallows and wandering albatross (*Diomedea exulans* L.) and giant petrel (*Macronectes giganteus* Gmelin and *M. halli* Mathews) nests support a luxuriant, dark-green *Poa cookii*-dominated vegetation which contrasts strikingly with the drab, yellow-green surroundings. The increased vitality of the influenced plants is directly correlated with increases in their nutrient contents due to excretion by these animals (Croome, R. L., unpublished 1971–2 expedition report).

The dominant plant cover of the well-drained slope areas of lowland black lava flows of Marion Island is that of a thick carpet of *Blechnum penna-marina* (Poir) Kuhn. On some protected slopes this fern carpet is replaced by a dense vegetation comprising luxuriant dark-green swards of *P. cookii* codominant with *Acaena magellanica* (Smith, 1976). A dense understorey of the moss *Brachythecium rutabulum* (Hedw.) B.S.G. occurs under the *Acaena* canopy and *Azorella selago* and *B. penna-marina* are common throughout this community, which has been termed *inland tussock grassland* by Huntley (1971) and which is invariably undermined by numerous burrows of small petrel and prion species.

Soils under these inland tussock grasslands have considerably higher contents of inorganic nitrogen (predominantly in the ammonium form) than do soils under plant communities not influenced by the birds (Table 1). It is felt that this is caused by addition of inorganic nitrogen to the tussock grassland soils through the bird excreta. In relation to their relatively low organic carbon values the total phosphorus content of these soils is also high, possibly indicating enrichment in inorganic phosphorus by the bird guano.

The total percentage base saturation of the tussock grassland soils is low compared with that of soils under other plant communities. This is principally due to lower exchangeable calcium and magnesium contents, which are associated with slightly lower pH values, in the tussock grassland soils. Tentatively, it is proposed that nitrification of the added ammonium ions in these soils causes the decrease in soil pH due to the reaction $2NH_4^+ + 4O_2 \rightarrow 2NO_3^- + 4H^+ + 2H_2O$ and that the newly formed nitrate ions are neutralized predominantly by calcium and magnesium to form soluble nitrate salts which are subsequently leached from the

TABLE 1

Chemical status of the horizons containing living roots in the soils under tussock grassland and non-tussock grassland plant communities.

Plant Communities	N	pH	% Water	% saturation of C. E. C. Ca	Mg	Na	K	Total	% Org.-C	% Total N	% Total P	mg/100 g soil NH_4–N	NO_3–N
Non-tussock grassland	22	4,2–4,7	674 ± 139,8	19 ± 3,1	28 ± 5,7	4 ± 0,6	4 ± 1,3	55 ± 9,2	34,3 ± 6,75	2,00 ± 0,280	0,65 ± 0,115	tr.–2,9	0,0–tr.
Tussock grassland	8	4,0–4,1	360 ± 19,4	14 ± 0,9	13 ± 2,5	5 ± 1,8	1 ± 0,4	34 ± 3,4	25,0 ± 3,96	1,66 ± 0,249	1,55 ± 0,381	0,9–8,4	0,0–1,0

Values expressed as ranges or as means ± 95% confidence limits.
N = number of determinations.
tr. = trace (< 1 mg/100 g soil).

upper soil horizons. This causes a further pH decrease and also explains the low calcium and magnesium status of soils under tussock grassland. This indirect evidence that nitrifying organisms are present, and are capable of functioning in the low pH-low temperature soil régime prevalent on the island, offers an interesting field for a microbiological investigation into the island's soil and peat deposits.

The exchangeable potassium status of these soils is very low, approximately 1%, corresponding to 0,1–0,4 m-equiv. of exchangeable potassium per 100 g of soil. Graley, Nicholls and Piper (1960) consider that soils possessing exchangeable potassium levels below 0,5 m-equiv. per 100 g soil may be suspect as being deficient in this element.

There are very marked differences in the nutrient status of tussock grassland and non-tussock grassland plants (Table 2). Dead and alive leaves of plants occurring in tussock grasslands have significantly higher contents of nitrogen, potassium, iron and, to a lesser degree, sodium than do plants of the same species from other, undisturbed plant communities.

Addition of nitrogen and phosphorus in the bird guano to the soils under tussock grasslands is probably directly responsible for the increased concentrations of these two elements in the plant leaves and also for the luxuriance and the high standing crops of tussock grassland communities (Smith, 1976). Potassium is involved in virtually every physiological function taking place within the plant (Ulrich and Ohki, 1966) and the increased concentration of this element in the roots and leaves of tussock grassland plants is thought to be a response to the greater plant vitality and growth caused by nitrogen and phosphorus fertilization rather than directly to addition of potassium to the system in the guano. It is of interest that the potassium content of the tussock grassland soils is lower than those of the soils under the other plant communities indicating that very little of this element is, in fact, added to the tussock grassland soils in the guano and that the increase in plant growth ''forced'' by the nitrogen and phosphorus fertilization causes increased plant uptake of potassium from a soil which can well be suspected as being deficient in this element.

No significant increases in soil sodium content due to manuring by the birds is evident in Table 1. The substantially higher sodium concentrations in some organs of the tussock grassland plants might therefore be a response to the low potassium concentrations of the underlying soils, as it is well known that in some plants partial replacement of potassium in the tissue may be assumed by sodium, especially where deficiencies of the former element occur (Ulrich and Ohki, 1966).

The concentrations of iron in alive and dead leaves of tussock grassland plants are consistently about two to three times higher than are those of plants of other slope areas, whereas no similar effect is apparent in the roots of the tussock grassland plants (Table 2). Early workers demonstrated the correlation between

TABLE 2

Comparison of the nutrient status of plants growing in inland tussock grassland and non-tussock grassland communities.

Species & Organ			Nutrient Content (%)													
	Site	N	Calcium		Magnesium		Sodium		Potassium		Iron		Nitrogen		Phosphorus	
			Mean	C.L.	Mean	C.L.	Mean	C.L.	Mean	C.L.	Mean	C.L.	Mean	C.L.	Mean	C.L.
Poa cookii																
Leaf	(1)	8	0,11	0,020	0,09	0,010	0,26	0,053	1,16	0,072	0,005	0,001	1,58	0,063	0,15	0,009
	(2)	4	0,12	0,026	0,09	0,016	0,27	0,070	*1,46	0,029	*0,018	0,012	*1,91	0,273	*0,18	0,014
Leaf litter	(1)	5	0,16	0,083	0,11	0,018	0,07	0,037	0,09	0,031	0,017	0,008	1,02	0,056	0,09	0,013
	(2)	3	0,14	0,126	0,11	0,040	*0,12	0,039	*0,25	0,049	*0,036	0,019	*1,35	0,108	*0,13	0,026
Root	(1)	4	0,15	0,098	0,12	0,044	0,20	0,085	0,40	0,032	0,076	0,007	1,24	0,143	0,12	0,013
	(2)	3	0,12	0,038	0,14	0,078	*0,32	0,111	*0,47	0,047	0,074	0,020	1,19	0,145	0,11	0,072
Acaena magellanica																
Leaf	(1)	5	0,75	0,107	0,51	0,054	0,38	0,098	1,25	0,209	0,008	0,002	1,95	0,069	0,22	0,007
	(2)	3	*0,64	0,047	0,53	0,172	*0,47	0,024	*1,63	0,216	*0,026	0,005	*2,16	0,152	*0,25	0,049
Leaf litter	(1)	5	0,91	0,225	0,54	0,045	0,16	0,062	0,31	0,035	0,016	0,006	1,85	0,130	0,17	0,006
	(2)	3	0,92	0,205	0,53	0,088	0,17	0,070	*0,43	0,100	*0,054	0,034	*2,24	0,322	*0,20	0,026
Root	(1)	5	0,19	0,052	0,24	0,060	0,06	0,031	0,54	0,023	0,023	0,033	0,93	0,065	0,11	0,030
	(2)	3	0,18	0,031	0,24	0,118	*0,11	0,041	*0,63	0,057	0,017	0,023	0,99	0,038	0,14	0,044
Azorella selago																
Leaf	(1)	8	0,48	0,097	0,35	0,064	0,94	0,198	1,26	0,077	0,014	0,004	1,38	0,156	0,14	0,013
	(2)	4	0,46	0,206	0,30	0,118	0,77	0,238	*1,91	0,126	*0,025	0,009	*1,65	0,025	0,13	0,037
Leaf litter	(1)	8	0,58	0,051	0,33	0,067	0,05	0,027	0,09	0,016	0,070	0,053	1,03	0,097	0,09	0,014
	(2)	4	0,49	0,034	0,25	0,022	0,02	0,025	0,07	0,016	*0,202	0,033	*1,27	0,095	*0,12	0,016
Root	(1)	5	0,42	0,110	0,39	0,059	0,19	0,054	0,81	0,138	0,018	0,005	1,32	0,028	0,14	0,018
	(2)	3	0,42	0,169	0,37	0,109	0,18	0,115	*0,98	0,035	0,014	0,014	*1,39	0,076	0,13	0,044
Blechnum penna-marina																
Leaf	(1)	11	0,44	0,048	0,070	0,029	0,25	0,062	1,42	0,031	0,004	0,001	2,39	0,143	0,25	0,020
	(2)	4	1,41	0,095	0,71	0,049	0,30	0,122	*1,74	0,102	0,004	0,001	*2,68	0,260	0,26	0,028
Leaf litter	(1)	11	0,80	0,113	0,89	0,024	0,12	0,035	0,19	0,014	0,014	0,002	1,79	0,060	0,19	0,012
	(2)	4	0,84	0,208	0,88	0,068	0,13	0,052	*0,27	0,062	*0,031	0,014	*2,11	0,262	0,19	0,055
Rhizome	(1)	6	0,33	0,030	0,40	0,068	0,20	0,085	0,79	0,158	0,025	0,018	1,32	0,147	0,21	0,066
	(2)	4	0,34	0,045	0,37	0,079	0,14	0,061	*1,15	0,102	0,020	0,014	N.D.		0,32	0,150
Brachythecium rutabalum																
Living fronds	(1)	4	0,42	0,232	0,35	0,066	0,10	0,026	0,81	0,066	0,030	0,015	1,71	0,182	0,14	0,058
	(2)	3	0,35	0,106	0,37	0,101	*0,16	0,050	*0,87	0,043	*0,065	0,037	*1,94	0,085	*0,21	0,030

(1) = mean element concentration ± 95% confidence limits (C.L.) in plants of non-tussock grassland communities.

(2) = mean element concentration ± 95% confidence limits (C.L.) in tussock grassland plants.

* indicates that the differences between (1) and (2) are significant at P = 0,5.

N.D. = not determined.

iron concentration and chlorophyll content in plant tissue (Bolle-Jones and Notton, 1954; Jacobson and Oertli, 1965) and it is now well established that the chloroplasts contain most of the iron in the leaf (Granick, 1958). The healthier, darker-green colour of the plants of tussock grasslands and other biotically influenced areas has been mentioned and it is felt that these increases in plant-colour intensity and plant vitality are directly associated with the higher iron concentrations in the leaves of the tussock grassland plants. This is supported by the absence of high iron concentrations in the roots of these plants. The low pH values (Table 1) and substantial iron pans and sesquioxide deposits which exist in the island soils make it unlikely that any of these soils are iron-deficient and that the guano is therefore supplying an essential requirement of the plants for this element.

The data in Table 2 indicates that *Acaena magellanica* leaves from tussock grasslands possess lower amounts of calcium than do those of non-tussock grassland communities. This is partly a reflection of the lower calcium status of the soils under tussock grassland (Table 1). *A. magellanica*, however, occurs abundantly in wet drainage-line communities which overlie (relatively) calcium-rich soils (Smith, 1976) and plants from these communities have high calcium contents. These high contents are principally responsible for the observed differences between the leaf-calcium status of tussock grassland and non-tussock grassland *Acaena* plants.

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